

## Delimitation of the series *Laurifoliae* in the genus *Passiflora* (Passifloraceae)

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### Abstract

Within the huge diversity of genus *Passiflora*, series *Laurifoliae* constitutes a strikingly uniform group, widely distributed in neotropical rain forests, at low to moderate elevations. Given its morphological and ecological unity, Killip mentioned it as an «exceedingly difficult» group. The lack of clear morphological criteria has not helped in delimiting it, and the confusion has grown with the addition of new species and criteria. As a preliminary step in the study of diversity within series *Laurifoliae*, we re-examine its morphological delimitation, assessing how its current 29 species (including the highly similar *P. pachyantha* and *P. killipiana*) conform to 20 criteria from different authors. Three criteria (indumentum on vegetative parts, stipule glands, membranous limen) appear to be irrelevant, because they are either too variable or rarely recorded in the species descriptions. Using the 17 remaining ones, 24 typical species show very limited variations, five of them differing by only one criterion. Among them, we retain terete to angular stem, setaceous or linear stipules soon deciduous, petiolar glands in one pair, leaves oblong, neither peltate nor lobate, three glandular bract over 1 cm long and free, flowers pendent, with two campanulate outer series of filaments (most other series much reduced or aborted). Five species, *P. guazumaefolia*, *P. kikiana*, *P. odontophylla*, *P. ischnoclada*, and *P. maliformis*, differ by three to nine traits, not found in the typical representatives of the series, so they can be excluded from it. *Passiflora kikiana* should be classified into series *Kermesinae*. For the four other ones, a satisfactory solution implies a more global study, involving other series.

### Introduction

Within Passifloraceae, the most important genus is *Passiflora* L. with about 588 species, distributed in tropical America as well as in South-Eastern Asia and Oceania (Krosnick *et al.* 2013). It contains lianas with tendrils, or shrubs and trees, with alternate leaves, axillary stipules, extra-floral nectaries on petioles and/or on leaf lamina, and flowers with an androgynophore and a corona of filaments (Ulmer & MacDougal 2004). Currently, 29 species have been assigned to series *Laurifoliae*, which is included in supersection *Laurifolia* (Cervi 1997) Feuillet & MacDougal of subgenus *Passiflora*, according to the classification of MacDougal and Feuillet (2004). In the latter, the level of morphological variation associated with each hierarchical level was not detailed.

In the previous classification, i.e., in ‘*American species of Passifloraceae*’, Killip (1938) divided *Passiflora* into 22 subgenera, further classified into sections and series. He described subgenus *Granadilla* (now subgenus *Passiflora*) as a group containing herbaceous or more rarely woody climbers, with generally large, entire or serrulate, bracts, organized in an involucre; flowers are usually large and highly colored; their calyx is campanulate, rarely short-tubular, and shorter than the sepals. Their coronas commonly bear two or more series of long and variegated filaments; their operculum is incurved, erect at margin, rarely erect throughout; the ovary is narrowed to the styles, or the styles arising at the top of ovary, free or united at their very base; fruits are often large. This subgenus was divided into 15 series, including series *Laurifoliae*. These series gather species with the greatest number of morphological characters in common. Killip (1938) neither detailed the characteristics of each series nor cited a type species for each one. Instead, he proposed a determination key to distinguish them.

Among them, the *Laurifoliae* appear as the most uniform one, which is why Killip (1938) qualified it as an “exceedingly difficult” group. At first sight, it also appears relatively uniform in its general ecology and distribution

in Amazonia, the biogeographic Chocó, and the Andean foothills, being associated with hot to moderately cool humid forest climates, between zero and ca. 2000 m of elevation. The fruits of *Laurifoliae* are greenish yellow to orange yellow and contain an appreciable quantity of edible, sweet and aromatic translucent pulp. Several species are cultivated for their fruits. *P. nitida* Kunth (1817, 130) is commonly cultivated in the Guianas. *P. laurifolia* Linnaeus (1753, 956) is mostly cultivated in the Caribbean; curiously it is not commercially cultivated in French Guiana, where it has been reported to grow wild. The Granadilla de Quijos, *P. popenovii* Killip (1922, 332), is highly prized in the Andes of Southern Colombia and Southern Ecuador. Thus, *Laurifoliae* species have a particular potential as a genetic resource for crop diversification and economic development (Yockteng *et al.* 2011).

Clear morphological series are particularly useful to understand radiations in *Passiflora*. Certain series, such as *Tiliifoliae*, correspond to the diffusion of a clear morphological pattern across different environments, with representatives in lowland humid and dry forests, as well as in montane forests. In contrast, species of series *Laurifoliae* follow an even stronger morphological pattern under more uniform conditions (humid forests at low to medium elevations), with a very wide geographic distribution and no clear indication of habitat fragmentation. Thus, series *Laurifoliae* provides a particular model for the study of the relationship between speciation and ecological adaptation. As a preliminary work for the revision of this series, we propose here to re-examine its morphological delimitation, mostly from literature data, confronting their original descriptions to the morphological criteria defining the series according to different authors. The description of *P. acuminata* and *P. guazumaefolia* has been completed by the examination of several specimens (see annexed list).

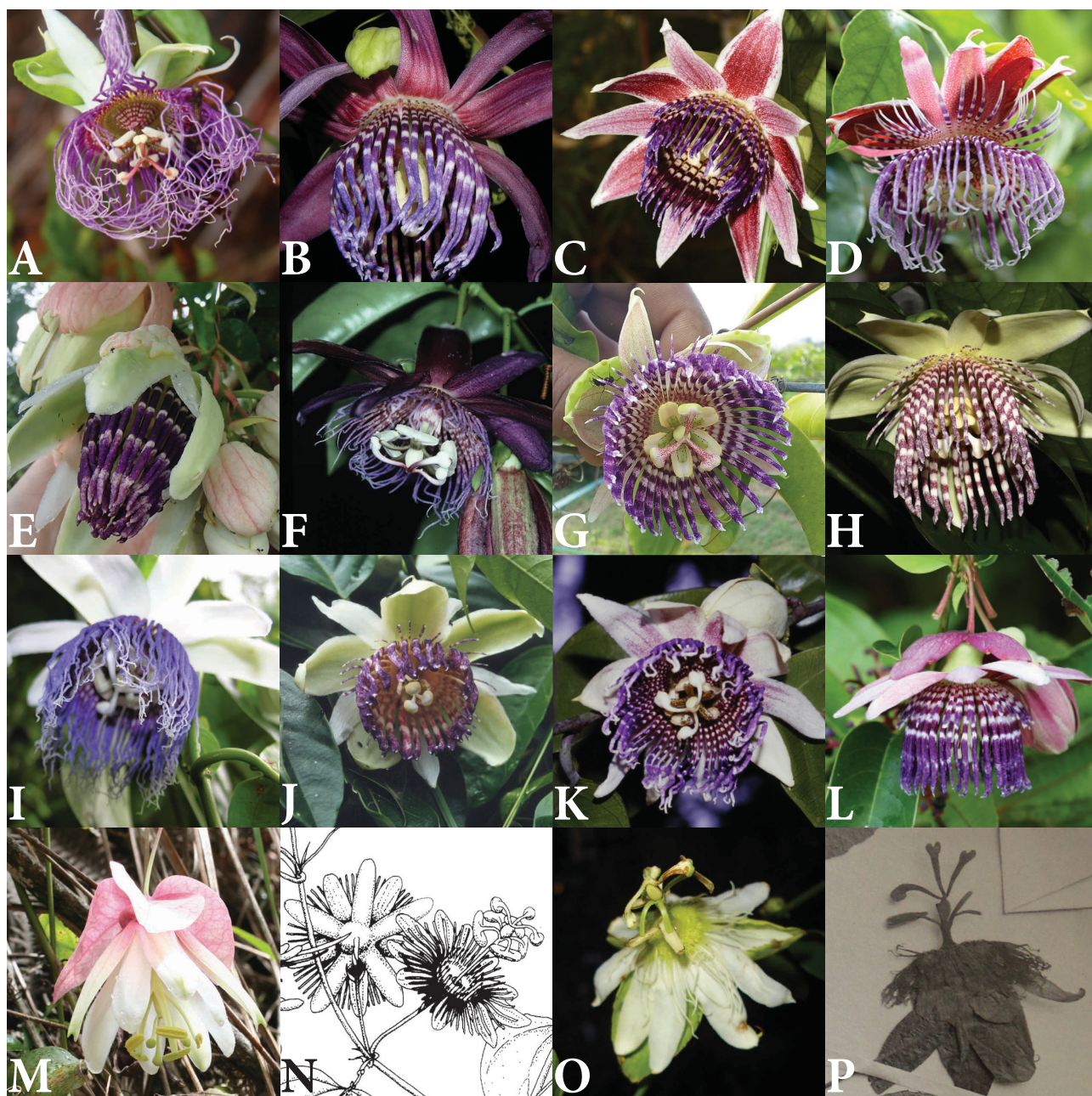
### Creation and taxonomic construction of series *Laurifoliae*

In 1938, series *Laurifoliae* included 13 species: *P. laurifolia*, *P. gleasonii* Killip (1924, 112), *P. tolimana* Harms (1894, 9), *P. nitida*, *P. capparidifolia* Killip (1924, 113), *P. riparia* Martius ex Masters (1872, 599), *P. popenovii* Killip, *P. ambigua* Hemsley (1902, 128), *P. guazumaefolia* Jussieu (1805, 112), *P. ischnoclada* Harms (1929, 812) (with reserves from Killip, because of poor condition of the type flower and resemblance of leaves and bracts with species of series *Simplicifoliae*), *P. odontophylla* Harms (1922, 296) ex Glaziov (1905, 315), *P. acuminata* DC (1828, 328), and *P. nigradenia* Rusby (1927, 311). They have stems that are terete to angular, not winged (vs. winged for the similar series *Quadrangulares*), bracts distinct to base (vs. united, at least at base in series *Digitatae* and *Tiliaefoliae*), stipules linear or setaceous, usually soon deciduous (vs. stipules foliaceous, semi ovate to semi oblong, attached on one side above base, often appearing reniform, in series *Kermesinae*, *Imbricatae*, *Simplicifoliae*, *Lobatae* and *Menispermifoliae*), leaves neither lobed nor parted (vs. 3–7 lobed, or compound, in series *Setaceae*, *Pedatae*, *Incarinatae* and *Palmatisectae*), bracts more than 1 cm long, rounded at apex, and leaves oblong or oblong-lanceolate, more than 2.5 cm wide, petioles biglandular (vs. bracts less than 1 cm long, acute; leaves lanceolate, less than 2.5 cm wide, and petiole glandless in series *Marginatae*). Finally, according to Killip (1938), the species of series *Laurifoliae* have no indumenta on their vegetative parts, which separates them from pubescent plants of series *Serratifoliae*.

Killip (1938) distinguished two main subgroups, one “with the outermost series of corona filaments much shorter than the next series,” “the other with the outermost filaments equaling or exceeding those of the next series.” Most generally, the distinctions among species follow particular combinations of these and other commonly variable traits: ovary pubescence, nectary gland position on the petiole (near the apex, close to the middle, or below the middle), operculum structure (membranous or filamentose). Few traits are unique to particular species: bract shape (small and narrow, acuminate in *P. gleasonii*), leaf apex (rounded in *P. capparidifolia*), peduncle length (8–10 cm in *P. popenovii*) and outer corona filament thickness (very slender in *P. acuminata*).

Contrasting with this homogenous pattern of variation where species can be distinguished on combinations of traits varying across the whole series, three species surprisingly present combinations of distinct traits that are rare in the series. Thus, the last description of *P. ischnoclada* mentions one or two pairs of petiolar glands, peltate leaves and coronas with outer series of filaments reduced to 5 mm (Bernacci, 2001, 197). *P. odontophylla* and *P. guazumaefolia* have flowers with outer series of filaments perpendicular to the androgynophore. The analysis of several *P. guazumaefolia* specimens reveals that its petiolar glands are shortly cylindrical and slightly cupuliform at apex while all other species have two sessile, discoid to oblong, glands. Another distinctive feature of *P. guazumaefolia*, *P. ischnoclada*, and *P. odontophylla* is the presence of a cylindric limen, distinct from the androgynophore base while others species have a reduced or absent limen. Figure 1 (M–P) present their diverse flowers, contrasting with the general pattern observed in flowers from 12 more typical species (A–L).





**FIGURE 1.** Flowers of the series *Laurifoliae*. A: *P. acuminata* (photo: J. B. Fernandes da Silva); B: *P. ambigua* (photo: R. Aguilar); C: *P. venusta* (photo: D. Scherberich); D: *P. cerasina* (photo: M. Vecchia); E: *P. crenata* (photo: M. Rome); F: *P. fissurosa* (photo: M. de Souza); G: *P. laurifolia* (photo: F. Booms); H: *P. nigradenia* (photo: D. Scherberich); I: *P. nitida* (photo: M. Rome); J: *P. popenovii* (photo: G. Coppens d'Eeckenbrugge); K: *P. rufostipulata* (photo: C. Houel); L: *P. gabrielliana* (photo: M. Rome); M: *P. ischnoclada* (photo: C. Houel); N: *P. kikiana* in Cervi (2010); O: *P. guazumaefolia* (photo: J. Ocampo); P: *P. odontophylla* (flower of the type specimen).

In 1939, Killip described *P. pachyantha* Killip (1939, 198) with all the characteristics of *Laurifoliae*, except that it is rufo-tomentous throughout. He noted that “clearly this species belongs to the subgenus *Granadilla*, but within that it does not go well into any of the fifteen series into which I divided that subgenus. It is best placed in a series by itself, coming between *Laurifoliae* and *Serratifoliae*, to which the name *Pachyanthae* may be given.” In 1960, describing *P. killipiana* Cuatrecasas (1960, 17) from Colombia, Cuatrecasas was confronted to the same problem. He excluded this species from the series *Laurifoliae*, for its ferruginous pubescence throughout, its minutely crenate leaves, larger bracts (4.5–5.5 cm long, 2–3 cm wide), thick and toothed, the size of the different parts of the flowers and the relative length of the successive filament rows of the corona. In his revision of the Brazilian passion flowers, Cervi (1997) gave a general description for series *Laurifoliae* in accordance with Killip’s classification (1938) and cited *P. laurifolia* as the type species of this series. One year later, Vásquez (1998) revised the *Laurifoliae* from Bolivia and added a diagnostic trait for the group: bracts with glandular margins.

**TABLE 1.** Morphological variation for criteria used for delimiting series *Laurifoliae*, based on published descriptions (*P. acuminata* by Killip (1938) ; *P. ambigua* by Killip (1938); *P. capparidifolia* by Killip (1938); *P. cerasina* by Annonay & Feuillet (1997); *P. chaparensis* by Vásquez (1998); *P. crenata* by Feuillet & Cremers (1984); *P. fernandezii* by Escobar (1989); *P. fissurosa* by De Souza & Hopkins (2011); *P. gabrielliana* by Vanderplanck & Laurens (2006); *P. gleasonii* by Killip (1938) ; *P. guazumaefolia* by Jussieu (1805); *P. ischnoclada* by Bernacci (2001); *P. kapiriensis* by Rome & Coppens (2016); *P. kikiana* by Cervi (2010); *P. killipiana* by Cuatrecasas (1960); *P. laurifolia* by Killip (1938); *P. maliformis* by Killip (1938) and Ulmer & McDougal (2004); *P. metae* by Bonilla *et al.* (2016); *P. nigradenia* by Vásquez (1998); *P. nitida* by Killip (1938); *P. odontophylla* by Killip (1938); *P. pachyantha* by Killip (1939); *P. pergrandis* by Holm-Nielsen & Lawesson (1987); *P. phellos* by Feuillet (2004); *P. popenovii* by Killip (1938); *P. riparia* by Martius (1872); *P. rufostipulata* by Feuillet (1986) a; *P. tolimana* by Killip (1938); *P. venusta* by Vásquez & Delanoy (2007). A light grey shade is used to underline trait variation in both typical and atypical species and three morphological criteria invalidated for their lack of consistency and/or documentation across the series (petiole nectar atrophy in *P. popenovii* is not considered significant). The darker grey shade is used to underline variations that are exclusive to atypical species (five rightmost columns).

source	morphological criteria	<i>P. acuminata</i>	<i>P. ambigua</i>	<i>P. capparidifolia</i>	<i>P. cerasina</i>	<i>P. chaparensis</i>	<i>P. crenata</i>	<i>P. fernandezii</i>	<i>P. fissurosa</i>	<i>P. gabrielliana</i>	<i>P. gleasonii</i>	<i>P. kapiriensis</i>	<i>P. laurifolia</i>	<i>P. nigradenia</i>	<i>P. nitida</i>	<i>P. pergrandis</i>	<i>P. phellos</i>	<i>P. popenovii</i>	<i>P. riparia</i>	<i>P. rufostipulata</i>	<i>P. metae</i>	<i>P. tolimana</i>	<i>P. venusta</i>	<i>P. killipiana</i>	<i>P. pachyantha</i>	<i>P. kikiana</i>	<i>P. odontophylla</i>	<i>P. guazumaefolia</i>	<i>P. ischnoclada</i>	<i>P. maliformis</i>
Killip (1938), Cervi (1997)	vegetative parts glabrous	+	+	+	+	+	+	-	+	+	+	+	+	+	+	+	-	+	+	+	+	+	+	-	-	-	+	+	+	+/-
	stem terete or angular, not winged	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	+	+	+	+	+	+	+	+	+	+	+	+	+
	stipules linear or setaceous, usually soon deciduous	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	?	+	+	+
	petioles biglandular	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+/-	+	+	+	+	+	+	+	-	+	+	+/-	+
	leaves oblong or oblong-lanceolate, entire or serrulate	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+/-
	leaves more than 2.5 cm wide	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	bracts distinct to base	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-
	bracts more than 1 cm	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	bracts rounded at apex	+/-	+	+	+	+	+	+	+	+	-	+	+	+	+	+	+	+	+	+	-	+/-	+	+	+	-	+	+	+	-
Vásquez (1998)	glandular bracts	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	+	+	-	-
Cervi (2010)	stipules with glands	?	?	?	?	-	?	?	?	?	?	?	?	-	?	?	?	?	?	?	+	+	-	?	+	+	?	?	?	-
	a campanulate calyx tube	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	a tubular or filamented operculum	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	a membranous limen	-	+	-	-	-	-	-	+	-	+	-	+	-	+	+	-	-	-	+	+	-	-	+	+	+	+	+	+	-
additional criteria	petiolar glands discoid to oblong, sessile	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	+	-	-	-
	leaves not peltate	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	+
	penninerved, secondary nerves alternate or sometimes opposite at leaf base	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	-	+	+	-
	three bracts in involucre	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	+	+	+	+
	flowers pendent	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	-	-	+	+
	2 outer campanulate series of filaments	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	-	-	-	+



In fact, most authors ascribing new species to series *Laurifoliae*, have not stuck to Killip's criteria. Thus, the classifications of *P. crenata* Feuillet & Cremers (1984, 378), *P. cerasina* Annonay & Feuillet (1997, 551), *P. pergrandis* Holm-Nielsen & Lawesson (1987, 501), *P. chaparensis* R. Vásquez (1998, 38) and *P. venusta* R. Vásquez & M. Delanoy (2007, 120) give no importance to their bract size, although it compares well with those of *P. killipiana*. Similarly, *P. fernandezii* L.K. Escobar (1989, 80), with its pronounced pubescence on young vegetative organs, as well as *P. phellos* Feuillet (2004, 285) and *P. fissurosa* Souza, M. A. D. (2011, 449), with their corky stems, were assigned to series *Laurifoliae*, together with more conform species, *P. rufostipulata* Feuillet (1986, 173), *P. gabrielliana* Vanderplank (2007, 237), *P. kapiensis* Rome & Coppens (2016, 8), and *P. metae* Bonilla *et al.* (2016, 129). When the current *Passiflora* classification was drafted and published (McDougal & Feuillet, 2003), *P. maliformis* Linnaeus (1753, 956) was transferred from series *Tiliifoliae* to series *Laurifoliae* (Ulmer & McDougal 2004, 300).

In 2010, along with his description and classification of *P. kikiana* Cervi (2010, 1062) in the series *Laurifoliae*, Cervi gave a broader description of the series: “herbaceous climbers with cylindrical stems and tendrils; petioles and stipules with glands; entire or lobed leaves, which are glabrous to sparsely tomentose; three bracts subtending the pedicels; a campanulate calyx tube; a tubular or filamented operculum and a membranous limen.” In fact, several characteristics of *P. kikiana* are unique in the series *Laurifoliae sensu* Cervi (2010): two or three pairs of stipitate glands on the petiole, asymmetrical membranous stipules, and bracts that are not arranged in an involucre. The outer series of short filaments perpendicular to the androgynophore is shared only with *P. odontophylla* and *P. guazumaefolia*. Thus, as a result of unstable classification criteria, there is no general agreement on the composition of series *Laurifoliae*. The reassessment of these criteria together with the assignment of species from 1938 to 2016, is a necessary first step in its revision.

### Interspecific morphological variation in *Laurifoliae*

We have compared the different species currently assigned to *Laurifoliae* based on the descriptions given by Killip (1938) for the first 13 species, and/or supplementary information from the descriptions of Cervi (2010) and Vásquez (1998). In total, our comparison concerns 29 species, after adding the two species that were not included in the series by Killip (1938) or Cuatrecasas (1939): *P. pachyantha* and *P. killipiana*. We also added new criteria from our own observations on series *Laurifoliae*.

The resulting synthesis, presented at Table 1, confirms that, globally, series *Laurifoliae* is morphologically homogeneous, except for five species: *P. kikiana*, *P. odontophylla*, *P. guazumaefolia*, *P. ischnoclada* and *P. maliformis*. All other, typical, species show negligible variation for most selected criteria. Two diagnostic traits distinguish only one species each: stem section does not apply strictly for *P. phellos*, whose terete stems are covered by cork ridges; biglandular petioles does not always apply for *P. popenovii*, as these glands are atrophied or even absent in some individuals or populations. Bract apex is rounded excepted in *P. gleasonii* (acuminate), *P. tolimana* (acute) and *P. metae* (ensiform bracts). Three criteria do not hold, either because they are most often not included in the descriptions (glandular stipules), or because they are too variable among the 23 typical species: glabrous vegetative parts (not applicable to four species) and membranous limen (not applicable to 14 species). Dismissing these three criteria, only four typical species differ from the other 19 ones, by no more than one of the remaining criteria.

Contrastingly, *P. guazumaefolia* differs for three validated criteria (short cylindrical glands on the petiole, erect flowers, with non campanulate corona), as well as *P. odontophylla* (erect flowers, with non campanulate corona, 3–5-nerved). *P. ischnoclada* differs by five criteria (petiole with two to three pairs of stipitate glands, peltate leaves, glandless bracts, non campanulate corona), *P. kikiana* by nine criteria (petiole with two to three pairs of stipitate glands, membranaceous and asymmetric stipules, glandless bracts, bracts ca. 1 cm, not in involucre, erect flowers, corona non campanulate, secondary nerves), and *P. maliformis* by five criteria (leaf shape and nervation, connate and glandless bracts, and petiolar gland shape).

### Discussion

In the genus *Passiflora*, the series corresponds to the taxonomical level immediately above the species. Following the work of Killip (1938), series gather species with the greatest number of morphological characters in common. From a statistical point of view, a group is correctly defined when differences among its species are smaller than differences with species of adjacent series. Thus, supersection *Laurifolia*, and its three main series, *Laurifoliae*, *Tiliifoliae*, and *Quadrangulares*, are well supported by the few species sampled in the morphological diversity study of Ocampo and

Coppens d'Eeckembrugge (2017), except for *P. guazumaefolia*, which is placed closer to species of supersections *Passiflora* and *Stipulata*.

According to our synthesis, three of the 20 diagnostic traits proposed by successive authors appear to be irrelevant (presence of indumentum on vegetative parts, glandular stipules, membranous limen), and we can dismiss them. Bract shape is a particular case: only three species descriptions mention non-rounded bract apices: *P. acuminata* (obtuse), *P. gleasonii* (cuspidate-acuminate), and *P. metae* (ensiform). According to Killip (1938), the former two only differ by bract shape and color, size of inner filaments, and operculum clefting; the possibility of infraspecific variation should be investigated before accepting them as diagnostic traits. For *P. metae*, it only differs from *P. gleasonii* and *P. tolimana* by bract size and shape. In case bract shape shows significant intraspecific variation in later studies, several of these species might fall in synonymy.

Using the remaining criteria, 24 species out of the 29 assigned to series *Laurifoliae*, show very limited variations, none of them differing from the others by more than one diagnostic trait. The five remaining species *P. guazumaefolia*, *P. kikiana*, *P. odontophylla*, *P. ischnoclada*, and *P. maliformis* differing by three to nine criteria from the 24 typical species, can be excluded from series *Laurifoliae*. A re-analysis of *P. kikiana* with the determination key of Cervi (1997) shows that it should be integrated into another series of subgenus *Passiflora*. With its cylindrical stems, its bracts free at base, its semi-oblong stipules and its three elliptical bracts, narrower than 0.5 cm and not arranged in an involucre, *P. kikiana* could be classified into series *Kermesinae*. The four others species are more difficult to reclassify and a satisfactory solution would necessitate a more global study.

## Conclusion

Several diagnostic characters used by Killip and Cervi (indumenta on vegetative organs, glandular stipules, bracts rounded at apex (with reservation), limen presence and shape), appear to be variable in the series, so they can still be used to differentiate species of the series, not to delimit the series. As a variable quantitative trait, leaf width is also questionable. The criteria “campanulate calyx tube” and “tubular or filamented operculum” are characters shared by all species of supersection *Laurifolia*. We can also exclude them from the definition of series *Laurifoliae*. These modifications allow restoring a homogeneous series *Laurifoliae*, which could be defined as follows:

Series *Laurifoliae*—Plants glabrous to pubescent. **Stems** terete to angular, wingless, sometimes corky on old parts. **Stipules** linear to setaceous, early deciduous. **Petiole** with two discoid to oblong sessile glands (except in populations of *P. popenovii*). **Leaves** unlobate, oblong-lanceolate, entire to glandular-serrulate, not peltate. **Bracts** three, in involucre, free at base, more than 1 cm long and glandular. **Flowers** pendent. **Outer series of filaments** two, campanulate (most other series much reduced or aborted).

Currently, series *Laurifoliae* includes 24 species corresponding to the above criteria: *P. acuminata*, *P. ambigua*, *P. cappariifolia*, *P. cerasina*, *P. chaparensis*, *P. crenata*, *P. fernandezii*, *P. fissurosa*, *P. gabrielliana*, *P. gleasonii*, *P. kapiensis*, *P. killipiana*, *P. laurifolia*, *P. metae* (when type effectively deposited), *P. nigradenia*, *P. nitida*, *P. pachyantha*, *P. pergrandis*, *P. phellos*, *P. popenovii*, *P. riparia*, *P. rufostipulata*, *P. tolimana*, and *P. venusta*.

## Herbarium specimens examined

### *P. guazumaefolia*:

Colombia: Bolivar, Municipality of Achi, 5 May 1987, Cuadros 3598 (MO); Municipality of San Martín de Loba, 24 July 1987, Cuadros 3781 (MO); orillas del DIque, 16 Jan. 1911, Dugand 2857 (MO); Dep. of Córdoba, Ciénaga de Ayapel, 10 July 1973, Idrobo 6579 (MO); Dep. Magdalena, Tenerife, in 1801, Humboldt sn (Holotype, P); Gamarra, 19 July 1952, Uribe 2405 (HUA), 18 July 1955, Uribe 2645 (HUA).

### *P. acuminata*:

Brazil: De Candolle sn (Type, P); Amazonas, Municipality of Manaus, Caracarai, 10 March 1978, Silva 4557 (INPA); along road from Manaus to Caracarai, 16 Aug. 1986, Croat 62222 (MO), Belem; Nov. 25 1942, Archer 7864 (K); South of Belem near mouth of Rio Guama, 14 Aug. 1986, Croat 62142 (MO).

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